THE ORIGIN AND EVOLUTION OF LIFE ON THE EARTH*

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LECTURE II, PART I

The Evolution of the Vertebrata

Chromatin evolution. Errors and truths in the Lamarckian and Darwinian explanations. Individuality in character origin, velocity and cooperation. Origin of the vertebrate type. The laws of convergence, divergence and of adaptive radiation in fishes and amphibians.

SIMON NEWCOMB[1] considered the concept of the rapid movement of the solar system toward Lyra as the greatest which has ever entered the human mind. The history of the vertebrates as the visible expression of the evolution of the microscopic chromatin presents a contrasting concept of the potentialities of matter in the infinitely minute state.

The peculiar significance of vertebrate chromatin is its stability in combination with incessant plasticity and adaptability to varying environmental conditions and new forms of bodily action; throughout constant changes of proportion, gain and loss of characters, genesis of new characters, there is always preserved a large part of the history of antecedent form and function, for chromatin is far more stable than the surface of the earth. In the vertebrates chromatin evolution is mirrored in the many continuous series of forms which have been discovered, also in the perfection of mechanical detail in organisms of titanic size and inconceivable complexity, like the dinosaurs among reptiles and the whales among mammals which rank with the *Sequoia* among plants.

There are two historic explanations of the causes of this wonderful process of chromatin evolution, each adumbrated in the Greek period of inquiry. The older, known as the Lamarckian, expressed in modern terms is that *the beginning of new form and new function is to be sought in the body cells* (*soma*), on the supposition that cellular actions,

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[1] Newcomb, Simon, "Astronomy for Everybody," Doubleday, Page & Co. November, 1902, 12mo, pp. 333.

reactions and interactions with each other and with the environment are heritable by the chromatin. This idea was originally suggested by the accurate observation of early naturalists and anatomists that bodily function not only controls form but is generally adaptive or purposive in its effects. According to this Lamarck-Spencer-Cope explanation a change of environment, of habit and of function should always be antecedent to changes of form in succeeding generations; moreover, if this explanation were the true one, successive changes in evolutionary series would be like growth, they would be observed to follow the direct lines of individual action, reaction and interaction, the young would be increasingly similar to the adults of antecedent generations, which is frequently the case but unfortunately for the Lamarckian explanation is not *invariably* the case.

The opposed explanation, the Darwinian, as restated by Weismann and De Vries, is that *the beginning of new form and function is to be sought in the germ cells or chromatin.* This is based upon the direct anti-Lamarckian view that the actions, reactions and interactions which cause certain bodily organs to originate, to develop, or to degenerate, to exhibit momentum or inertia in development, are not inherited and do not give rise to corresponding sets of predispositions in the chromatin. According to this explanation all predispositions to new form and function not only begin in the germ cells but are more or less lawless or experimental, they are constantly being tested or tried out by bodily experience, habits and functions. Technically stated they are fortuitous variations followed by selection of the fittest variations. Thus Darwin's disciple, Poulton, also De Vries, who has merely restated in his law of "mutation" Darwin's original principle of 1859, and Bateson, the most radical thinker of the three, hold the opinion that there is no adaptive law observed in variation but that the chromatin is continuously experimenting and that from these experiments selection guides the organism into adaptive and purposive lines.

ENVIRONMENTAL CORRELATION, ADAPTATIONS OF RESPIRATORY, OLFACTORY, VISUAL, AUDITORY, THERMAL, GRAVITY FUNCTIONS AND ORGANS
TO VARIATIONS OF LIGHT, HEAT, HUMIDITY, ARIDITY, CAUSED BY MIGRATIONS OF THE INDIVIDUAL OR OF THE ENVIRONMENT, COÖRDINATIVE AND CORRELATIVE

INTERNAL CORRELATION
CORRELATION AND COÖRDINATION OF THE INTERNAL GROWTH AND FUNCTIONS THROUGH INTERNAL SECRETIONS (ENZYMES) AND THE NERVOUS SYSTEM

ADAPTATIONS TO NUTRITION
(1) ON INORGANIC COMPOUNDS
(2) ON BACTERIA
(3) ON PROTOPHYTA, ALGAE, ETC.
(4) ON PROTOZOA
(5) ON HIGHER PLANTS, HERBIVOROUS DIET
(6) ON HIGHER ANIMALS, CARNIVOROUS DIET
(7) PARASITIC, WITHOUT OR WITHIN PLANTS AND ANIMALS

ADAPTATIONS TO INDIVIDUAL COMPETITION AND SELECTION
(A) SELECTION, AFFECTING VARIATION, RECTIGRADATION, MUTATION, ORIGIN AND DEVELOPMENT OF SINGLE CHARACTERS, PROPORTIONS, ETC.
(B) AFFECTING ALL REPRODUCTIVE ORGANS. PRIMARY AND SECONDARY

ADAPTATIONS OF RACIAL COMPETITION AND SELECTION
AFFECTING CHIEFLY ALL MOTOR, PROTECTIVE, OFFENSIVE, AND DEFENSIVE STRUCTURES OF THE ENDO- AND EXOSKELETON; ALSO REPRODUCTION RATE

a. The peculiar significance of vertebrate chromatin is its stability in combination with incessant plasticity and adaptability to varying environmental conditions and new forms of bodily action.

Neither the Lamarckian nor the Darwinian explanation accords

with all that we are learning through paleontology and experimental evolution of the actual modes of the origin and development of adaptive characters. That there are elements of truth in each explanation is evident from the following. Adaptive characters present three phases: first, the *origin* of character-form and character-function; second, the more or less rapid *acceleration* or *retardaton* of character-form and function; third, the *coordination* and *cooperation* of character-forms and functions. If we adopt the physico-chemical theory of the origin and development of life it follows that the causes of such origin, velocity (acceleration or retardation) and cooperation must lie somewhere within the actions, reactions and interactions of the four physico-chemical complexes, namely, the physical environment, the developing organism, the chromatin, the living environment, because these are the only reservoirs of matter and energy we know of in life history. While it is possible that the relations of these causes will never be fathomed, it is certain that our search must proceed along the line of determining which actions, reactions and interactions invariably precede and which invariably follow, those of the body-cells (Lamarckian view) or those of the chromatin (Darwinian-Weismann view).

The Lamarckian view that adaptation in the body cells *invariably* precedes similar adaptive reaction in the chromatin is supported neither by experiment nor by observation; such precedence while occasional and even frequent is by no means invariable. The Darwinian view, namely, that chromatin evolution is a matter of fortuity and displays itself in a variety of directions, is contradicted by paleontological evidence both in the Invertebrata and Vertebrata, among which we observe that continuity in chromatin evolution prevails over the evidence either of fortuity or of sudden leaps or mutations, that *in many characters there is a prolonged rectigradation or direct evolution of the chromatin toward adaptive ends.* This is what we mean in saying that in evolution law prevails over chance.

Darwin's quest for the origin of *species* having become an incidental issue, the chief quest of evolutionists to-day is the origin and history of *single characters.* The discoveries of modern paleontology are in accord with many of the recently discovered laws of heredity, which will be described in the succeeding course of the Hale Lectures. Paleontology supports heredity in demonstrating that every vertebrate organism is a mosaic of an inconceivably large number of "characters" or "character-complexes," structural and functional, some indissolubly and invariably grouped and cooperating, others singularly independent. For example, every one of the most minute scales of a reptile or hairs of a mammal is a "character complex" having particular chemical formulæ and chemical energies which condition the shape, the color, and the function and all other features of the complex. Through re-

searches on heredity each of these character complexes is now believed to have a corresponding physico-chemical determiner or group of determiners in the germ chromatin, the chromatin existing not as a miniature but as an individual *potential and causal.*

The *principle of individuality,* namely, of separate development and existence, which we have seen to be the prime characteristic of the first chemical assemblage into an organism (p. 179), also governs each of these character complexes. In some vertebrates we observe an infinity of similar character complexes evolving in an exactly similar

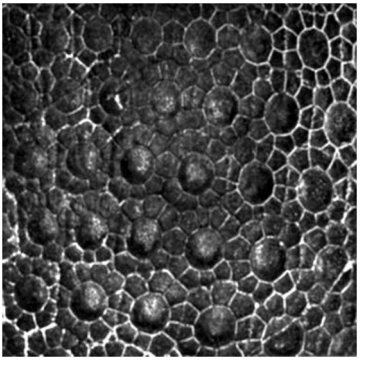

FIG. 1. SHELL.

FIG. 2. TOOTH.

manner, as in the beautiful markings of the shell and the exquisite enamel pattern of the teeth of the glyptodon, in which every portion of the shell evolves similarly, and every one of the teeth evolve similarly, from which we might conclude that there is an absence of individuality in form-characters and that some homomorphic (similarly formative) impulse is present in all characters of similar ancestry; but this rash conclusion is offset by the existence of other character complexes of similar ancestry which each evolve differently, or are in a high degree heteromorphic (diversely formative), as, for example, in the grinding teeth of mammals.

This individuality and separability inherent in character-form is equally observed in character-velocity, and is at the basis of the shifting of characters and of all the proportionate and quantitative changes which make up four-fifths of vertebrate evolution. For example, two character-forms side by side may evolve with equal velocity and maintain a perfect symmetry or one may be accelerated into very rapid

momentum,[2] while the other may be retarded into a state of absolute inertia or equilibrium. These are the extremes of character-velocity which result in the states known as *development, balance* and *degeneration.* In many parts of the skeleton development and degeneration so obviously follow use and disuse that Cope was led to propose a law of Bathmism (growth force) and to explain the energy phenomena of use and disuse in the body tissues as the *cause* of the appearance of corresponding energy potentialities in the chromatin. In other words, that the energy of development or of degeneration in the bodily parts of the individual is inherited by corresponding parts in the germ. As pointed out above, the defect in this supposed law consists in its not being invariably applicable.

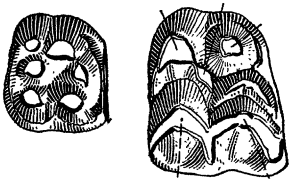

FIG. 3. FIRST UPPER MOLAR OF *Meniscotherium terræ rubræ.*

FIG. 4. FIRST UPPER MOLAR OF *Euprotogonia puercensis.*

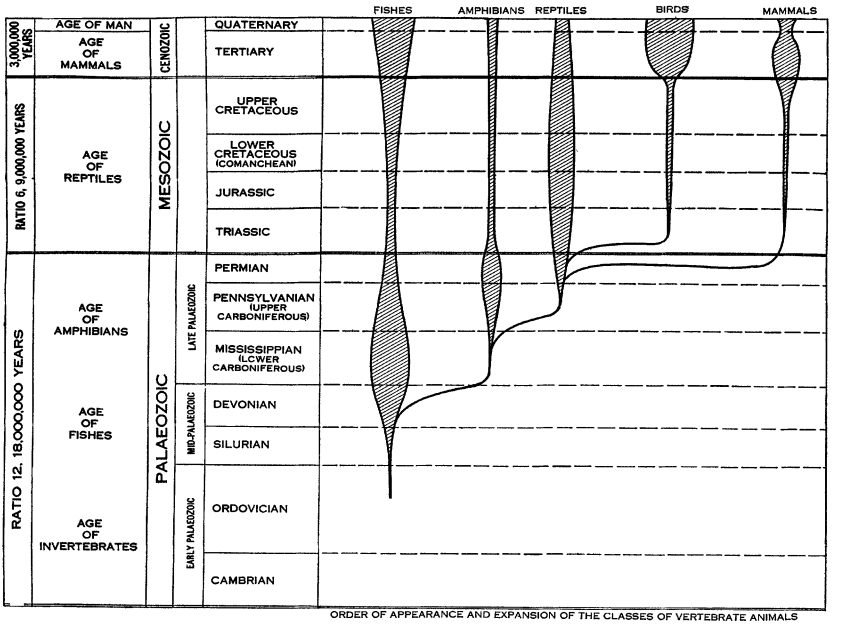

FIG. 5. ORDER OF GEOLOGIC APPEARANCE AND EPOCHS OF MAXIMUM ADAPTIVE RADIATION (EXPANSION) AND DIMINUTION (CONTRACTION) OF THE FIVE CLASSES OF VERTEBRATED ANIMALS. Prepared by Osborn and Gregory.

[2] In physics momentum equals mass × velocity. In biology momentum and inertia refer to the relative rate of character change both in individual development (ontogeny) and in evolution (phylogeny). *Character-parallax* would express the differing velocities of two characters. Thus the character-parallax of the right and left horns in the Brontotheriinæ (titanotheres) is very small, *i. e.,* they evolve at nearly or quite the same rate; on the other hand, the character-parallax between the premolar teeth in these animals is very great. The char-

Changing bodily form and function and the ever changing velocity in character-complexes is to be regarded as an expression of physico-chemical energy resulting from the actions, reactions and interactions of different parts of the organism, and, as repeatedly stated in these lectures, the only vista which we enjoy at present into the causes of character-origin, character-velocity and character-cooperation is through chemical catalysis, namely, through the hypothesis that actions and reactions of form and of motion liberate specific catalytic messengers in the nature of ferments, enzymes, hormones, which produce specific and cooperating interactions in every character-complex of the organism. In our survey of the marvelous evolution of the vertebrates we may constantly keep in mind the concept of the actions, reactions and interactions of the hard parts of the structural tissues, which are preserved in fossils. In this field of observation the chemical and physiological influences of the body can only be inferred and the relations of these physico-chemical influences to those of the chromatin are absolutely unknown. Yet changes in the bodily hard parts invariably mirror the evolution of the chromatin, in fact, this evolution is nowhere revealed in a more extraordinary manner than in the incessantly changing characters in such hard parts as the labyrinthine foldings of the deep layers of enamel in the grinding teeth of the horse. This evolution of the hard parts in adaptation resolves itself into six chief and concurrent phenomena, namely:

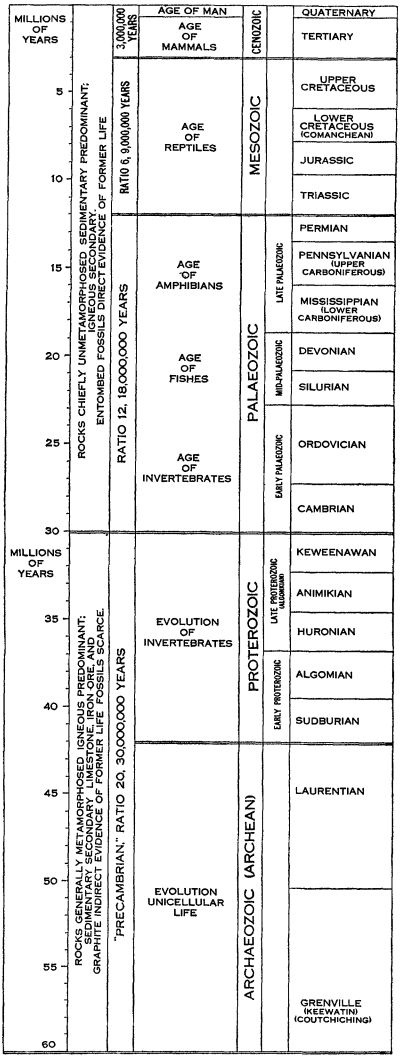

FIG. 6. GEOLOGIC TIME SCALE. Prepared by the author and C. A. Reeds after Schuchert.

acter-parallax idea has innumerable applications and can be expressed quantitatively.—W. K. GREGORY.

Ever changing character form and character-function,
Ever changing character-velocity in individual development and in the chromatin,
Ever changing character-cooperation, coordination and correlation,
Incessant character-origin in the chromatin, sometimes following, sometimes antecedent to character-origin in the organism,
Relatively rapid disappearance of character-form and -function in the individual,
Relatively slow disappearance of character-form and -function in the chromatin.

} Characters and Character-Complexes

FORM EVOLUTION OF THE VERTEBRATES UNDER THE MECHANICAL AND PHYSICO-CHEMICAL ACTIONS, REACTIONS AND INTERACTIONS OF LOCOMOTION, OFFENSE AND DEFENSE, AND REPRODUCTION[3]

Ordovician time, the early Paleozoic epoch next above the Cambrian, is the period of the first known vertebrates, the fossil remains of fish dermal defenses found near Cañon City, Colorado, as announced by Walcott in 1891, and subsequently in the region of the present Big Horn Mountains of Wyoming and the Black Hills of South Dakota. Small spines referred to Acanthodian sharks are also abundant in the Ordovician of Cañon City, Colorado. Since they were slow-moving types protected with the beginnings of a dorsal armature composed of small calcareous tubercles, to which the group name Ostracoderm refers, probably these earliest known pro-fishes were not primitive in external form but followed upon a long antecedent stage of vertebrate evolution. In the form-evolution of the vertebrates relatively swift-

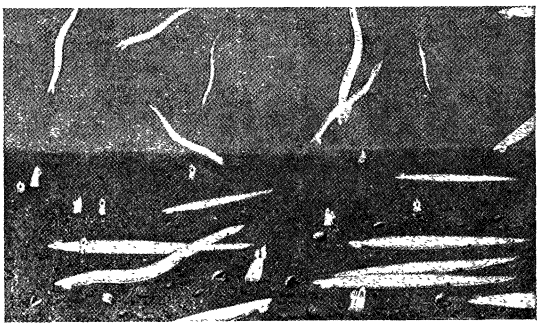

FIG. 7. THE EXISTING LANCELETS (*Amphioxus*), fusiform protochordates, living in the littoral zone the sole survivors of an extremely ancient stage of vertebrate evolution. After Willey.

moving, defenseless types are invariably antecedent to slow-moving, armored types.

Ancestral to these Ordovician vertebrates were free-swimming,

[3] For the geologic history the author is chiefly indebted to his fellow academician, Charles Schuchert. For the latest knowledge regarding the evolution of the vertebrates to his Columbia University colleague, William K. Gregory.

quickly darting types of unarmored fishes. The double pointed, fusiform body, in which the segmented propelling muscles are external and a stiffening notochord is central, is the fish prototype, which more or less clearly survives in the existing lancelets (*Amphioxus*) and in the larval stages of the degenerate Ascidians. These animals furnish numerous embryonic and larval proofs of descent from nobler types.

Taking the whole history of vertebrate life from the beginning, we observe that every prolonged adaptive phase in a similar habitat becomes impressed in the hereditary characters of the chromatin, which throughout the development of new adaptive phases always retains more or less potentiality of repeating the embryonic, immature, and even the mature structures of older adaptive phases of older environments. The chromatin is at once the most conservative and the most progressive center of physico-chemical evolution; it records past adaptations, it meets the emergencies of the present through the adaptability which it imparts to the organism in its distribution throughout every living cell; it is continuously giving rise to new characters and functions. This law of ancestral repetition, formulated by Louis Agassiz

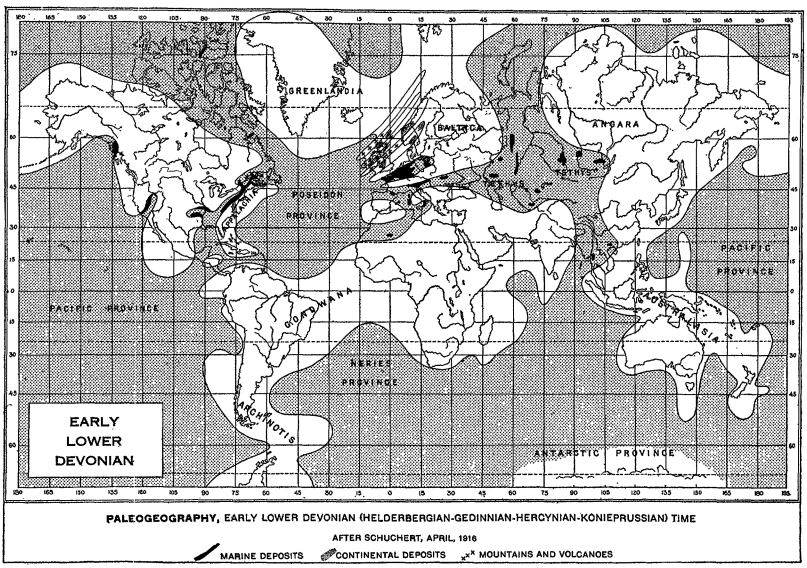

FIG. 8. PERIOD OF THE EARLY APPEARANCE OF TERRESTRIAL INVERTEBRATES AND VERTEBRATES. Paleogeography of the earth in early Lower Devonian time, showing the hypothetical southern continent *Gondwana* and the Eurasiatic inland sea *Tethys*, according to the hypotheses of Suess. After Schuchert, 1916.

and developed by Haeckel and Hyatt, dominated biological thought during thirty years of the nineteenth century (1865–1895), and with more or less success a highly speculative solution of the ancestral history of the vertebrates was sought in embryonic development and com-

parative anatomy long before the actual lines of evolutionary descent were determined through paleontology.

The form-evolution of the backboned animals, beginning with these pro-fishes of Cambrian and Pre-Cambrian time, extends over a period of 30,000,000 years. The supremely adaptable vertebrate body type begins to dominate the living world, overcoming one mechanical difficulty after another as it passes through the habitat zones of water, land and air. Motions necessary for the capture, storage and release of plant and animal energy continue to control the form of the body and of its appendages, but in the meantime the organism through mechanical and chemical means protects itself either offensively or defensively and also adapts itself to reproduce and protect its kind, according to Darwin's original conception of the struggle for existence as involving both the life of the individual and the life of its progeny. Among all defenseless forms speed is a prime necessity, while all heavily armored forms gradually abandon mobility. As among the Invertebrata, calcium carbonate and phosphate and various compounds of keratin and chitin are the chemical materials of armature. Locomotion, as distinguished from that in all invertebrates, is in an elongate body stiffened by a central axis. The evolution of the skeletal supports (endoskeletal) and limbs is generally from the center of the body (notochord) toward the periphery, the evolution of the defensive armature (exoskeleton) is from the periphery toward the center. The defensive armature finally, through change of function, makes important contributions to the inner skeleton.

THE LAW OF CONVERGENCE OR PARALLELISM IN LOCOMOTOR, OFFENSIVE AND DEFENSIVE ADAPTATIONS

Although the structural body type and mechanism of locomotion is profoundly diverse, there arise hundreds of adaptive parallels between the Vertebrata and the antecedent evolution of the Invertebrata. The combined necessity for protection and locomotion brings about close parallels in body form between such primitive Silurian eurypterids as *Bunodes* and the vertebrate Ostracoderms, a superficial resemblance which has led Patten[4] to defend the view that the two groups are genetically related.

The theoretic application of the fundamental law of action, reaction and interaction becomes increasingly difficult as adaptations multiply and are superposed upon each other with the evolution of the four physico-chemical relations, as follows:

[4] Patten, Wm., "The Evolution of the Vertebrates and their Kin," 8vo, P. Blakiston's Son & Co., 1912, 486 pp., 309 figs.

Physical environment, succession, reversal and alternation of habitat zones,	Incessant Selection and Competition
Individual development, succession, reversal and alternation of adaptive phases,	
Chromatin evolution, addition of the determiners of new adaptations while preserving the determiners of old adaptations,	
Succession of life environments.	

Yet it must be the similarity of these internal physico-chemical energies of protoplasm and the similarity in the mechanics of motion, of offense and defense, which underlies the law of convergence or parallelism in adaptation, namely, *the production of externally similar forms in adaptation to externally similar natural forces,* a law which escaped the keen observation of Huxley[5] in his remarkable analysis of the modes of vertebrate evolution published in 1880.

The whole process of motor adaptation in the vertebrates, whether the fishes, amphibians, reptiles, birds, or mammals, is the solution of a series of mechanical problems, adjustment to gravity, overcoming the resistance of water or air in the development of speed; in the evolution of the limbs of creating levers, fulcra (joints) and pulleys. The fore and hind fins of fishes and the fore and hind feet of mammals evolve uniformly where they are homodynamic and divergently where they are heterodynamic. This principle of homodynamy and heterodynamy applies to the body as a whole and to every one of its parts, according to two laws: first, that each individual part has its own mechanical evolution, and, second, that the same mechanical problem is generally solved on the same principle. This we observe is invariably the ideal principle, for unlike man nature wastes little time on inferior inventions but immediately proceeds to superior inventions.

The three mechanical problems of existence in the water habitat are: first, overcoming the buoyancy of water either by weighting down, increasing the gravity of the body, or by the development of special gravitating organs which enable animals to rise and descend in this medium; second, the mechanical problem of overcoming the resistance of water in rapid motion which is accomplished by means of warped surfaces and well-designed entrant and reentrant angles of the body similar to those of the fastest modern yachts; third, the problem of propulsion of the body, which is accomplished, first, by sinuous motion of the entire body terminating in the powerful propulsion of the tail fin, secondly, by supplementary action of the four lateral fins, third, by the horizontal steering of the body by means of the median system of fins.

[5] Huxley, T. H., "On the Application of the Laws of Evolution to the Arrangement of the Vertebrata, and more Particularly of the Mammalia," *Proc. Scientific Meetings of the Zoological Soc. of London for the year 1880,* pp. 649–662. (Read December 14, 1880.)

The terrestrial and aerial evolution of the four-limbed types (Tetrapoda) is designed chiefly to overcome the resistance of gravity and in a less degree the resistance of the atmosphere through which the body moves. When the aerial stage evolves, with increasing speed the resistance of the air becomes only slightly less than that of the water in the fish stage, and the warped surfaces, the entrant and reentrant angles evolved by the flying body are similar to those of the rapidly moving fishes.

BRANCHING OR DIVERGENCE OF FORM, THE LAW OF ADAPTIVE RADIATION

In general the *law of divergence* of form, perceived by Lamarck and rediscovered by Darwin, has been expanded by Osborn into the modern *law of adaptive radiation,* which expresses the differentiation of animal form radiating in every direction in response to the necessities of the quest for nourishment and the development of new forms of motion in the different habitat zones. *Divergence* is constantly giving rise to differences in structure, while *convergence* is constantly giving rise to resemblances of structure. In contrast with this divergent principle is the *convergence* brought about by the similarity above described of the physico-chemical laws of action, reaction and interaction and the similarity of the mechanical obstacles encountered by the different races of animals in similar habitats and environmental media.

The chief advance which has been made in the last fifty years is our abundant knowledge of the *modes* of adaptation as contrasted with the very limited knowledge yet attained as to the *causes* of adaptation. The law of adaptive radiation is a law expressing the modes of adaptation of form, which falls under the following great principles:

Law of Adaptive Radiation of Form

1. Divergent adaptation, by which the members of the primitive stock tended to develop differences of form while radiating into a number of habitat zones.
2. Convergent adaptation, whereby animals from different habitat zones enter a similar habitat zone and acquire many superficial similarities of form.
3. Direct adaptation, for example, in primary migration through an ascending series of habitat zones, aquatic or terrestrial, arboreal, aerial.
4. Reversed adaptation, where secondary migration takes the reverse direction from aerial to arboreal, to terrestrial, to aquatic habitat zones.
5. Alternate adaptation, where the animal departs from an original habitat and primary phase of adaptation, and then returns from the secondary phase of adaptation to a more or less perfect repetition of the primary phase by returning to a primary habitat zone.
6. Symbiotic adaptation, where vertebrate forms exhibit reciprocal, or interlocking adaptations with the evolution of other vertebrates or invertebrates.

Prolonged residence in a single habitat zone results in profound alterations in the chromatin, and in consequence the history of past phases is more or less clearly recorded. It is very important to keep in mind that the body and limb form developed in each adaptive phase is the starting point of the next succeeding phase.

Among the disadvantages of prolonged zonal existence are the following. Through the law of compensation, discovered by Geoffroy St. Hilaire early in the last century, every vertebrate in developing and specializing certain organs sacrifices others; for example, the lateral digits of the foot of the horse are sacrificed for the evolution of the central digit as the animal evolves from tridactylism to monodactylism. These sacrificed parts are never regained; the horse can never revert to the tridactyl condition although it might reenter the habitat zone in which three digits on each foot would serve the purposes of locomotion better than one. In this sense chromatin evolution is irreversible. The extinction of vertebrate races has generally been due to the fact that the various types have sacrificed too many characters in their physiological reactions to a particular life habitat zone. A finely specialized form representing a perfect mechanism in itself which closely interlocks with its physical and living environment reaches a *cul de sac* of structure from which there is no possible emergence by adaptation to a different physical environment, or habitat zone. It is these two principles of the non-revival of characters once lost by the chromatin and of too close adjustment to a single environment which underly the law that the highly specialized and most perfectly adapted types become extinct, while primitive, conservative and relatively unspecialized types invariably become the centers of new adaptive radiations.

HABITAT MIGRATIONS OF THE INDIVIDUAL
MIGRATIONS OF THE ENVIRONMENT

AËRIAL
(FLYING, VOLANT, TYPES)

AËRO-ARBOREAL
(PARACHUTE, GLISSANT, TYPES)

ARBOREAL
(CLIMBING, LEAPING, BRACHIATING TYPES)

ARBOREO-TERRESTRIAL
(WALKING AND CLIMBING, SCANSORIAL, TYPES)

TERRESTRIAL
(AMBULATORY, SLOW; CURSORIAL, RAPID; SALTATORY, LEAPING; GRAVIPORTAL, SLOW, CUMBROUS. MUTIPEDAL. QUADRUPEDAL, BIDEDAL, APODAL, ETC.)

TERRESTRIO-FOSSORIAL
(WALKING AND BURROWING TYPES)

FOSSORIAL
(BURROWING TYPES)

TERRESTRIO-AQUATIC
(AMPHIBIOUS TYPES)

AQUATIC
(SURFACE-LIVING, BOTTOM-LIVING, SWIFT-CURRENT, SLOW-CURRENT)

FLUVIATILE
(FRESHWATER, FLUVIO-MARINE TYPES)

LITTORAL
(SURFACE AND FOSSORIAL TYPES)

PELAGIC
(FREE SURFACE-LIVING, DRIFTING, FLOATING, SELF-PROPELLING TYPES)

ABYSSAL
(DEEP BOTTOM-LIVING TYPES. SLOW AND SWIFT-MOVING)

b. THE THIRTEEN CHIEF VERTEBRATE HABITAT ZONES, each of which is divided into many subzones.

(*To be continued*)